OBSERVATIONS ON THE BEHAVIOR OF THE HOLOTHURIAN, THYONE BRIAREUS (LESEUR).[1]

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I. Introduction.

The different classes of echinoderms show in a remarkable way the extreme variations which one fundamental plan of structure may undergo in order to become adapted to different conditions of existence. Developing from a bilaterally symmetrical pelagic larva, the adult echinoderm becomes an almost perfect type of radiate symmetry, except in those forms which have a bilaterality superposed secondarily upon the typical radiate plan of structure, so that the adult becomes bilaterally symmetrical only after it has passed through the more primitive

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bilateral and radiate stages. Correlated with the variations in structure which are found in this group of animals, are corresponding differences in locomotion, respiration, feeding and other life processes, and the behavior of echinoderms is therefore a matter of particular interest on account of the opportunity it offers to compare the reactions of nearly related forms which have somewhat different types of symmetry. The reactions of certain stelleroids and echinoids (which are typically radiate in structure) have been carefully studied, but no observations of behavior have been made on holothurians (which are more or less bilateral) except for the brief papers of Clark ('99) and Grave (:02, :05). The writer had the opportunity, during July and August of the present year, of observing the common sea-cucumber, *Thyone briareus* (Leseur), and though lack of time prevented the observations from being very extensive and left many questions untested, it is believed that there are some points of interest in what follows. The object of the work was (1) to determine what the normal activities of this holothurian are and (2) to discover how its reactions are influenced by external stimulation. The experiments were carried on in the Marine Biological Laboratory, at Woods Hole, Mass., and my thanks are due to the director, Professor F. R. Lillie, for his kindness during the work.

II. Structural Characteristics.

In order that we may have clearly in mind the structural peculiarities of the form with which we are dealing and to gain an idea of the points in which it has departed from the typical radiate plan of symmetry, some time will be devoted to a brief review of the anatomy. *Thyone briareus* (Fig. 1) is a spindle-shaped animal which varies considerably in size, and this variation is not only dependent on the age but also on the condition of contraction or expansion. Fully extended individuals sometimes measure over twenty centimeters in length and a specimen of this size would be only six or seven centimeters long when contracted. At the posterior end there is an opening through which water is drawn into the cloaca and expelled again for purposes of respiration and excretion. The mouth is at the anterior end and is surrounded by

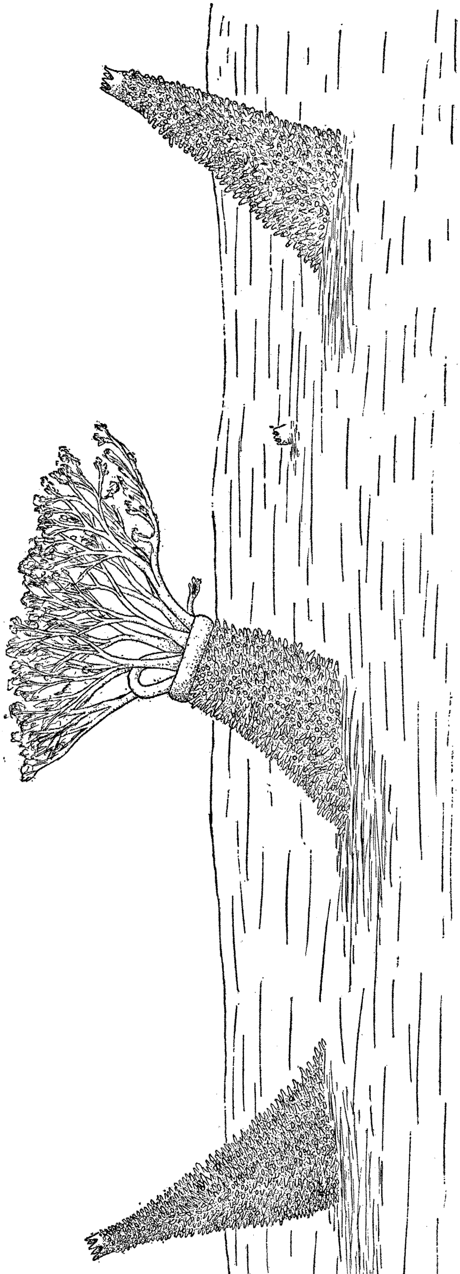

FIG. 1. *Thyone briareus.* Sketch representing three individuals buried in the mud. *A* is fully extended and both ends are visible. *B* has only the tip of the posterior end uncovered but *C* projects somewhat further above the mud.

ten dendroid tentacles which may be extended for feeding or collapsed and completely concealed by the turning in of the anterior end of the body. Just behind the tentacles is a "collar" which is without the slender tube-feet which cover the rest of the body. The tube-feet on the ventral and lateral surfaces have well developed sucking discs at their tips but such adhesive organs are not uniformly present on the dorsal side of the body. Besides this difference in the tube-feet, the dorsal and ventral surfaces may be distinguished from each other by the fact that the former is shorter than the latter and hence the ends of the body turn upward when the animal rests on its ventral side. They may be further distinguished by the difference in color (ventral being lighter), by the presence of a single median dorsal genital papilla between the bases of the tentacles, and by the fact that the two ventral tentacles are much shorter than the others. The internal organs are strikingly bilateral in their arrangement. This is shown by the right and left respiratory trees which unite and have a common opening on the dorsal side of the cloaca, by the single dorsal gonad and madreporite, and by the ventral Polian vesicles. The organs of the body wall are, on the other hand, typically radial in arrangement and hence the skeletal, muscular, water-vascular and nervous systems conform in general to the usual echinoderm type of structure. The water-vascular and nervous systems both consist of a circum-oral ring from which five radial branches extend in the body wall to the region of the cloaca. The skeletal parts consist of ten ossicles around the mouth which together form "the lantern," and of minute calcareous plates imbedded in the skin at the anterior and posterior ends of the body. The muscular system consists of five longitudinal bands, which extend from the circum-oral ossicles to the posterior end of the body, and of circular muscles which lie just beneath the skin and completely fill the space between the longitudinal muscles. The digestive tube is considerably coiled and is differentiated into four regions: an œsophagus which passes through the lantern, an expanded stomach, a slender intestine, and a musular cloacal chamber which gives rise dorsally to the respiratory trees.

From this brief synopsis of the structure of *Thyone*, it will be seen that, though we are dealing with an animal having a radiate

plan of structure, it has been modified in such a way that all of the systems of organs are more or less bilateral. There are well-differentiated anterior and posterior ends, but these are at the extremities of an axis which is horizontal instead of vertical as in most other echinoderms, for, like all holothurians, this species rests on its ventral side and the oro-anal axis is hence parallel to the surface on which it lies.

III. Methods of Response to Stimuli.

The behavior of any animal consists of the reactions which it gives in response to changes in its environment or to changes in its internal condition. It is an easy matter to change the surrounding conditions but we can interpret the internal changes which an animal undergoes as it responds to various stimuli only by its movements. Every species is limited to certain types of response by its structure, by the medium in which it lives, and by its past history. Therefore the first question to be considered is, by what reactions is *Thyone* able to respond when it is stimulated? The chief types of response will be stated briefly and the consideration of how they are brought about left for later discussion.

1. *Withdrawing Reaction.* — The reaction which is most often seen is the withdrawal of the posterior end of the body and the closing of the cloacal opening. The extent of this response depends upon various factors and it may be so slight as to be barely noticeable or it may be so marked that the body entirely disappears beneath the sand in which the animal is buried and remains out of sight for two or three minutes. Similar withdrawing reactions are performed by the anterior end of the body and also by the isolated parts, such as a single tube-foot.

2. *Extending Reaction.* — Under certain conditions the posterior end of the body becomes greatly elongated and is sometimes stretched as much as nine centimeters above the mud in which an individual lies buried.

3. *Locomotion.* — If *Thyone* is placed on a hard surface, such as the bottom of a glass dish, it attaches the tube-feet and moves across the surface and it may even climb the side of the dish. It is also able to burrow into sand or mud and may move about somewhat beneath the surface.

4. *Change in Size.* — As has been previously stated, this species undergoes marked changes in size and may shrink to a half or a third of its original volume when it is strongly stimulated.

5. *Feeding.* — Under certain conditions the circum-oral tentacles are extended and either waved in the water or swept over the surface of the mud in which the animal is buried. They are then consecutively poked into the mouth and wiped off. This reaction has been briefly described by Grave (:02).

6. *Change in Respiratory Movements.* — Water is periodically drawn through the cloacal chamber into the respiratory trees and expelled again. This series of breathing movements may be interrupted for a time or the rate may be increased or decreased.

7. *Self Mutilation.* — When the water becomes stagnant or when conditions become otherwise unfavorable the anterior end of the body is often cast off together with some of the visceral organs. The lantern, the circum-oral nerve and water vascular rings, the tentacles, and more or less of the enteric canal are frequently lost in this manner.

There are then at least seven well-defined reactions which may be used as a basis for the study of the behavior of *Thyone.* None of these responses are invariably called forth, however, when an individual is subjected to a certain stimulus. While one reaction is taking place it may exert an inhibitory influence on others, and the responses are all more or less changeable and therefore apt to vary in degree with a repetition of the same stimulus.

IV. Locomotion.

1. *On a Solid Surface.* — Individuals which were moving on a solid surface were never observed to extend the tentacles and remained more or less contracted so that they were usually not more than seven or eight centimeters long. When an animal is placed on the bottom of a dish in sea water it remains contracted for a short time, but the ventral tube-feet usually become attached within a minute. The posterior end is then slowly extended and the respiratory movements begin; the tube feet are protruded on all sides of the body and begin to wave about, and those which come in contact with a solid object attach themselves. The animal may move in any direction but the locomotion usually carries

it away from the source of the light, as *Thyone* is very sensitive to photic stimulation. Locomotion is brought about by shortening the tube-feet after they have been extended and attached, by twisting and extending movements of the whole body, and it is also assisted by sharp waves of muscular contraction which travel from one end of the body to the other.

The tube-feet act by pulling. They were never observed to become rigid enough to lift the body from the surface on which it rested, nor was there any pushing action, such as Jennings (:07, p. 99) described in the starfish. There was some lack of correlation in their movements and this manifested itself in two ways. When locomotion was taking place in a definite direction, the tube-feet were not only extended on the side towards which the animal was moving, but also over all the rest of the body. This was doubtless due partly to the fact that the tube-feet serve as organs of touch as well as of locomotion, but there were nevertheless a large number of seeking movements which were apparently of no use in locomotion. Furthermore, some of the tube-feet which were behind as an individual moved often remained attached for some time after they could be of any help in locomotion, and, after being greatly stretched, they were actually jerked from their attachments with a snap. They were never torn loose from the body, however, as often happens when *Arbacia* is pulled away from a solid surface. The stimulation which brings about the attachment of the terminal discs of the tube-feet is apparently contact with a solid object. Bits of shell, sand, and other bodies were frequently held by them for several days at a time.

In addition to the pulling action of the tube-feet, locomotion was often assisted by movements of the body. Individuals sometimes assumed a shortened form, detached the tube-feet at one end of the body, and then elongated this free end or made slow seeking movements which were somewhat like those of a leech. This free portion of the body was then attached and the animal slowly regained its contracted form again, thus making some progress. The sharply defined waves of contraction which commonly passed from one end of the body to the other were apparently of use chiefly in enabling the tube-feet to gain a new

attachment. A constriction might appear at either end as a ring around the body and pass to the opposite end. These rings usually moved over the body singly and a new one appeared about every three minutes on an active individual. Sometimes constrictions appeared simultaneously at both ends and neutralized each other as they met in the middle. As one of these constricted rings moved along the tube-feet were pulled from their attachments and folded into it, and when they were again extended they became fastened at points farther along in the direction of locomotion. As has been stated, *Thyone* apparently experienced some difficulty in getting the tube-feet to detach themselves at the proper time and this "ring-of-constriction" method was entirely effective in simultaneously pulling them loose in a certain region of the body. It is not intended to intimate however that the tube-feet could not be detached and moved forward without the use of these periodic constrictions.

Perhaps the most striking feature of the locomotion on a solid surface was the fact that it was without definite orientation. Individuals moved with the posterior end in advance as often as with the anterior end, and although the long axis of the body was as a rule approximately parallel with the direction of locomotion, animals often moved a long distance (as much as 12 cm.) with the body at right angles to the direction of movement, that is, they moved straight toward the right or left. The rate of locomotion was slow, the most rapid movement recorded being seven centimeters in fifteen minutes, or nearly half a centimeter per minute. In climbing up a vertical surface like the side of a dish the movements were not essentially different from those which took place when an individual was creeping on a horizontal surface.

2. *Burrowing.* — When *Thyone* is placed in a dish of sea water on a sandy bottom it usually twists and turns the body until it comes in contact with the side of the vessel. It attaches itself to the side, burrows downward, and then moves away from the side of the dish into the sand. The tube-feet are apparently of little use in locomotion on sand, and this fact supports the conclusion reached from watching their action on a solid surface, that they are effective in pulling the body along rather than in pushing

it. Occasionally individuals were found which burrowed directly into the sand without attaching themselves to any solid object. The results of an experiment performed on July 25 are typical of the other cases of burrowing observed. Four animals were placed in aquarium jars containing sand and sea water. One individual burrowed straight down into the sand and covered itself in three hours; another lay on top of the sand two hours and then took four hours to burrow; the third individual twisted about on top for half an hour, then came in contact with the side of the jar and burrowed into the sand in two hours and a half; the fourth took four hours to reach the side and then partly covered itself in two hours. On another occasion an animal lay on the sand eighteen hours but covered itself in two hours when placed against the side of the jar.

Burrowing is accomplished by a contraction of the body muscles and the action of the tube-feet. When the body is fastened to some solid object, the tube-feet are attached as far down its side as possible and the body is drawn out so that it is wedge-shaped in cross-section. The longitudinal body muscles are then contracted so that the body shortens, and the sand is forced aside as the cross-section becomes more circular in outline. During the entire process the two ends of the body are turned upward and the animal sinks down into the sand with the dorsal surface constantly uppermost. This method of procedure is usually repeated until the individual is completely buried, except the posterior end. The downward movement is assisted by the passage of constricted rings from one end of the body to the other, or from both ends toward the middle, the sand thus being loosened so that the body can be "wedged" down into it. When there is no solid object for the attachment of the tube-feet, burrowing is more difficult. As the waves of contraction pass over the body, the sand is gradually pushed aside so that a thin portion of the ventral surface is forced downward (Fig. 2, *A*). The dorsal longitudinal muscle bands and the circular muscles then contract and the ventral portion of the body expands in such a way that the sand is forced aside (*B*). This same process is repeated at intervals until the animal is covered.

Thyone can move about to some extent after it is buried in the

sand. It accomplishes this in the same way that it burrows and also to some extent by bending and straightening the body. A series of experiments was carried out to ascertain how deep *Thyone* could be buried in the sand and yet burrow out. The method was to place an individual in the bottom of a jar containing sea water to a depth of 55 cm., which was the height of the jar. It was then covered with sand to the desired depth. Individuals

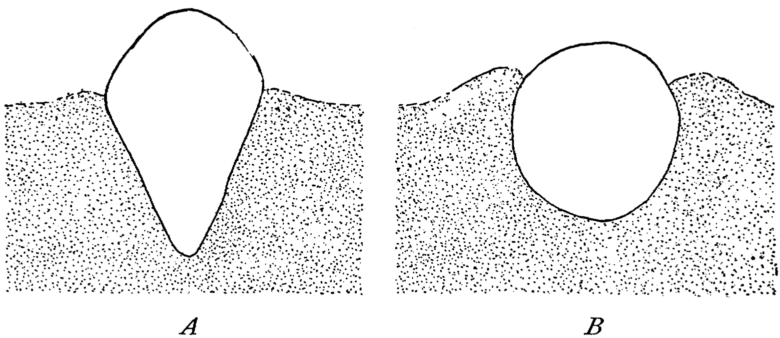

FIG. 2. Diagrams representing the shape of cross-sections in the middle of the body of *Thyone* as it burrows into the sand. The form shown in *A* precedes that shown in *B*.

were able to come to the top of the sand when covered under fifteen centimeters but none came up through twenty centimeters although ten large individuals were tested.

Clark ('99) found that *Synapta* burrowed with the tentacles and that it always went into the sand "head first." *Thyone* differs from it quite strikingly in the latter respect but this difference is perhaps no more than would be expected from the structural unlikeness between the two forms.

V. Feeding.

After an individual has been undisturbed for some time it often extends the anterior end of the body and the tentacles and makes feeding movements (Fig. 1, *A*). In this extension the longitudinal muscles pull the lantern forward and the circular body muscles contract. The anterior end of the body is thus everted, like the turning inside out of the finger of a glove. The branched tentacles are then pushed out by the pressure of the fluids within them and the action of the muscles in their walls.

The two short ventral tentacles are most active and constantly move in and out of the mouth opening, while the larger tentacles wave about more slowly. The latter are moved through the water or scraped over the bottom and then consecutively wiped off in the mouth. When one of these large tentacles is wiped off, its proximal end is pushed into the mouth first and the distal branches follow. Before one tentacle has emerged, another is usually being pressed down upon it ready to enter. Sometimes two of the large tentacles bend toward the mouth at once but in no case were two seen to enter the mouth simultaneously, one of them always bending back after a moment to make way for the other. The eight large tentacles are used in a more or less regular sequence, and in general it may be said that the one which has been out of the mouth longest and which is farthest from the tentacle which is emerging will be the next to enter the mouth. They are seldom used in the exact order one would expect from this statement however. For example, those nearest the muddy bottom are usually more frequently used than the others. Many observations were made as to the sequence in the wiping of

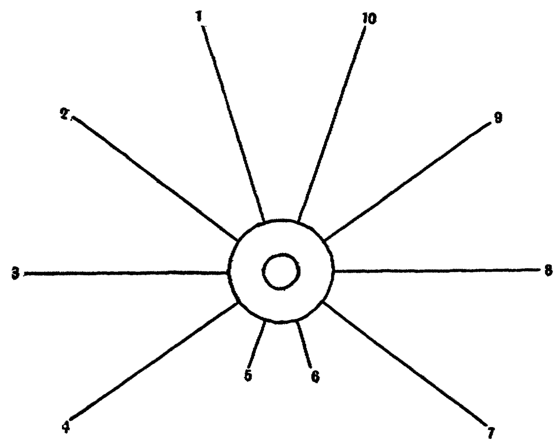

FIG. 3. Diagram to show the arrangement of the tentacles around the mouth as seen in an anterior view.

the tentacles and the following series is a typical one (see Fig. 3): 2, 7, 1, 4, 10, 8, 3, 9; 7, 2, 1, 4, 10, 8, 3, 9; 2, 7, 1, 4, 10, 8, 3, 9; 7, 2, 4, 1, 7, 10, 3, 4, 8; 2, 7, 9, 1, 3, 9, 7, 1, 8, 3, 10, 2, 8, 1, 7, 4, 8, 3, 10, 2. In this series a rather regular se-

quence is shown in the use of the tentacles. Number 7 was used eight times; numbers 1, 2, 3, 8, seven times; numbers 4 and 10, six; and number 9, five times. The time required for the fifty-three reactions was nine minutes and thirty seconds. A little over ten seconds was therefore required for the wiping of each tentacle. No account was taken of the two ventral tentacles in this series as they kept moving in and out almost constantly and without any apparent relation to movements of the others. In another larger series the different tentacles were used the following number of times: No. 1, twenty-one; No. 2, sixteen; No. 3, fourteen; No. 4, twelve; No. 7, eleven; No. 8, fourteen; No. 9, twenty-one; No. 10, nineteen. In this case tentacles 1, 10 and 9 were nearest the surface of the sand and they were used most frequently while those on the opposite side of the mouth (3, 4, 7) were less often employed. The time for this series of one hundred and twenty-eight reactions was fifteen minutes and thirty seconds, seven and a quarter seconds being required for the wiping of each tentacle.

The feeding reaction usually occurred only after an individual had been undisturbed for some time and when it was partly buried in the mud or sand, but animals were sometimes observed to feed when attached to the side of a jar. No stimulus was found which would cause *Thyone* to extend the tentacles and feed. Attempts were made to induce animals to perform the feeding reaction by allowing crab or fish extract to flow gently over the anterior end; and by using mud from the place where they were collected, but such stimuli were without results or caused only the withdrawing reaction. In one instance, however, a positive reaction was observed. In this case a small portion of a bryozoan colony (*Bugula*) was dropped in such a way that it fell upon the anterior end of a partly buried individual. The tentacles were at once extended and the anterior end of the body was bent over so that they scraped the point where the stimulation had occurred. This experiment was repeated many times and on different individuals but no other positive reaction was induced. From these observations it may be concluded that the feeding reaction occurs only after the animal has been undisturbed for a time and is probably brought about mostly by internal factors, such as hunger.

Thyone's food consists of the microscopic organisms and debris to which the tips of the branching tentacles adhere. Such materials are wiped off as the tentacles are thrust into the mouth and extended again. The stomachs of seven freshly collected individuals were examined on August 10 and found to contain: living protozoans (*Lichnophora*, *Gymnodinium*), nematodes and diatoms (several species); filamentous and unicellular algæ; pieces of plant tissue; encysted protozoans; two harpacticid copepods; and an ostracod. *Thyone* is apparently a rather indiscriminate feeder but sand was infrequent in the stomach contents and, though particles of sand were seen sticking to the tentacles as they entered the mouth, most of them were brought out again as the tentacles emerged.

VI. Respiratory Movements.

Thyone carries on a regular system of breathing movements by which water is taken into the cloacal chamber and expelled again. The general plan of this chamber is shown in median longitudinal section in Fig. 4. There are three openings from

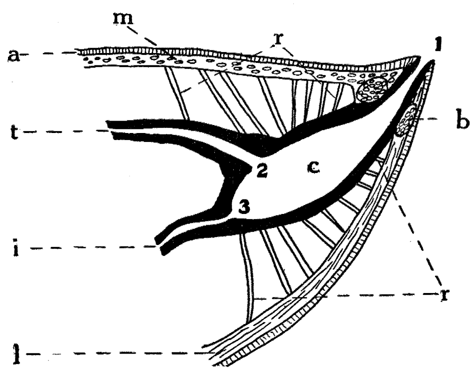

FIG. 4. Diagram representing a median longitudinal section through the posterior end of the body. *a*, integument; *b*, sphincter muscle; *c*, cloacal chamber; *i*, intestine; *l*, longitudinal body muscle; *m*, circular body muscles; *r*, radial muscles; *t*, respiratory trees. *1*, opening into cloacal chamber; *2*, opening into respiratory trees; *3*, opening from intestine.

the cloacal chamber *c*. These lead to the exterior *1*, to the respiratory trees *2*, and to the intestine *3*. During respiration the opening from the intestine *3* into the cloaca usually remains closed and takes no part in the breathing movements. Water is

drawn into the cloacal chamber by closing the opening to the respiratory trees *2* and contracting the radical muscles *r*, which extend from the cloaca to the body wall. The cloacal opening *1* is then closed, the respiratory tree aperture *2* is opened, and the contraction of the walls of the cloaca forces the water into the respiratory trees. Sometimes the cloacal opening *1* is kept closed while the water is forced back and forth from the cloaca to the respiratory trees, but the water is usually expelled from the body after each inspiration. When an individual is placed in shallow water so that the terminal opening *1* is just below the surface, the water is often expelled with enough force to form a fountain-like "spout" 3 or 4 cm. high.

The rate of the spouting reactions varies considerably, as is shown by the following observations, made upon two individuals which were buried in the sand. The average time between 144 consecutive spouting movements was 39 seconds for one animal; and the average time between 24 spouts was thirteen seconds for the other. In order to ascertain what would happen if these two individuals were prevented from spouting for a long period of time, they were first observed as they lay buried in the sand and the rate of their normal respiration noted. They were then made to pull the posterior end down into the sand by poking it with a glass rod, and whenever it started to emerge it was poked so that it was again withdrawn. The first animal spouted every twenty seconds (seven times) before being prevented from breathing and was then kept under the sand for one hour and twenty minutes. After the posterior end had appeared again there were no spouting movements for four minutes, and the next seven spouts averaged 36 seconds apart. The other animal averaged thirteen seconds between 24 spouts before its breathing was prevented. It was kept under the sand for two hours, 36 minutes and forty seconds; and at the end of that time it spouted with the posterior end still buried in the sand. The next nineteen spouts averaged one minute and five seconds apart. In both these instances the rate of respiration was more rapid before the breathing movements were prevented than afterwards. That is, an individual breathed more slowly after it had been made to "hold its breath" for an hour or two than it had before. This result can be accounted

for by the fact that the movements which force the water into the respiratory trees were more forcible after the period passed without respiration and hence they required a longer time. In addition to the respiratory movements described there is doubtless an exchange of gases through the integument and *Thyone* could probably exist for some little time without spouting.

VII. Responses to Stimulation.

Having completed the consideration of locomotion, feeding, and respiration, attention will now be directed toward some of the responses which result from such forms of stimulation as can be controlled by the experimenter.

1. *Tactile Stimulation.* — *Thyone* is extremely sensitive to contact with solid objects. If an animal is twisting about on the surface of the sand and comes in contact with a solid surface, the tube-feet are immediately extended and attached. Furthermore, if an individual is placed in a glass dish, it comes to rest in the angle between the bottom and side, where the body has the greatest surface in contact. When the contact stimulus is received from a moving object, the characteristic withdrawing reaction is given and the response varies with the stimulus. The tip of a glass rod may be gently pressed against the side of an individual if the movement is very gradual but the same pressure will cause a marked response if suddenly applied. The following experiment is a good example of sensitiveness to jars and other slight disturbances. A drop of water was allowed to fall from a height of one meter into a one-liter beaker containing a feeding individual. As soon as the drop struck the surface of the water above the animal, the tentacles were withdrawn and the cloacal opening was closed.

There is great variability in the sensitiveness of different individuals and those which had been in the laboratory for some time often allowed the tentacles to be touched with a glass rod whereas freshly collected individuals would contract at any slight jar, such as the closing of a door. Grave (:05) obtained similar results from his study of *Cucumaria.*

2. *Gravity.* — *Thyone's* responses to gravity were tested in two ways, by the righting reaction and by locomotion on an inclined

surface. The righting reaction is one of the most characteristic activities of this species. If an individual is placed in a flat-bottomed dish containing sea water and held with its ventral side uppermost until the tube-feet have attached themselves (usually about half a minute), it slowly pulls the body over with the tube-feet until the ventral surface is against the bottom of the dish. The tube-feet are helped to perform this righting reaction by the rings of muscular constriction which pass slowly from one end of the body to the other. The direction of the turning is determined by various factors, light being an important one. For example, when an individual rests on its dorsal surface with the long axis of the body at right angles to the direction of the light, the ventral surface is usually turned away from the light as the body is righted.

In order to test the locomotor reactions on an inclined surface four individuals were each given four consecutive trials in the

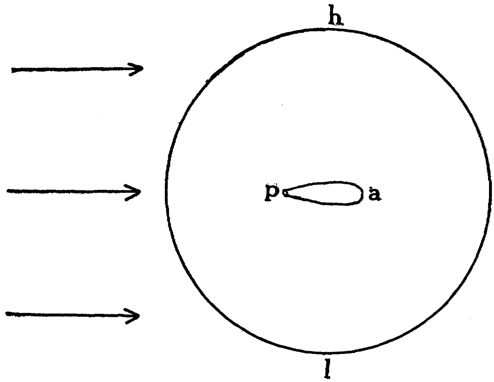

FIG. 5. Diagram showing the position in which individuals were placed in the dish during experiments to test the locomotion on an inclined surface. The arrows represent the direction of the light. *a*, anterior end ; *h*, high side of dish ; *l*, low side of dish ; *p*, posterior end.

bottom of a round glass dish, which measured thirty centimeters in diameter and contained sea water. This dish was placed directly in front of a window which was the only source of light in the room and the bottom was tipped 5.6° from the horizontal at right angles to the direction of the light rays. Animals were placed separately in this dish with the long axis of the body parallel to rays of light (Fig. 5). They were first given two trials with the bottom of the dish

inclined toward the left, the anterior end of the body being placed toward the window in the first case and away from it in the second. The dish was then inclined toward the right and the same procedure repeated. The distance from the center to the edge of the dish was fourteen centimeters and directions which the different individuals took in reaching the latter are shown in Table I. These results do not show any strongly geotropic tendency and the next step would naturally have been to test individuals on an inclined surface with the light coming from above or to make similar tests in total darkness but lack of time prevented such experiments being carried out.

TABLE I.

Deflection in moving fourteen centimeters away from the light on a plane surface inclined 5.6° at right angles to the direction of the light rays.

Direction of Locomotion.	Straight away from Light.	Up Incline.	Down Incline.
Individual No. 1		10°	
		10°	
	+		
			5°
Individual No. 2			90°
		90°	
		10°	
	+		
Individual No. 3	+		
	+		
	+		
	+		
Individual No. 4			10°
			22°
			10°
			5°
Total reactions	6	4	6
Average deflection	0	30°	24°

3. *Chemical Stimuli.* — No extensive experiments to test reactiveness to chemical substances were made. It was hoped, however, that positive responses might be obtained by using food substances, but repeated experiments with fish and crab extract, crushed eel-grass and scrapings from the surface of the mud were without results. The reactions which resulted when the water became foul were doubtless due to chemical stimuli. In this case individuals extended the posterior end of the body until the cloa-

cal opening was near the surface of the water, or came out of the sand and climbed up the side of the jar in which they were kept, or increased the size of the body and ceased to respond to shadows and other slight stimuli, and in some cases even cast out the visceral organs.

4. *Change in Density of Medium.* — *Thyone* can stand a marked increase or decrease in the density of the water in which it lives without serious interference with its activities. In order to test the effect of increased density an individual was placed in a one-liter beaker which had sand in the bottom to a depth of six centimeters. This beaker was filled with sea water and allowed to remain on the table in the laboratory from July 12 until August 7 (twenty-five days), when the animal died. During this time the water had evaporated so that the specific gravity had increased from 1.024 to 1.052. This animal showed no signs of the changes due to unfavorable environment until July 1, when it came out of the sand where it had been previously buried and lay on top. From this time it began to show signs of degeneracy, the skin was blistered off in spots and the body took on a peculiar elongated form. Many of the reactions continued to be normal however and the usual shadow reaction (which is described in the next section, p. 277) was easily induced the day before it died. On the morning of August 7 the animal failed to respond to shadows but gave the withdrawing response when it was poked gently. Four hours later it was dead. Subsequent examination showed that the visceral organs were still in place and had not been cast out on account of the increased density of the water.

The effects of a decrease in density were next investigated. Individuals were placed for a time in various mixtures of sea and fresh water. They were then returned to sea water and their subsequent condition noted. The results of these experiments are shown in Table II. No individual ever attempted to burrow while it was in a solution of lesser density than sea water, although sand was always placed in the bottom of the dish. The body remained contracted, spouting was infrequent and the tube-feet were never attached and seldom even extended over much of the body surface. In the cases where the animals survived their immersion in the mixtures they soon began regular spouting move-

ments after being replaced in sea water and gave typical, burrowing, feeding and shadow reactions within a few hours. The visceral organs were cast out in only one case and that was after an individual had been left in perfectly fresh water for three hours.

TABLE II.

Results of experiments in which *Thyone* was placed in mixtures of fresh and sea water.

Parts, by Volume, used for Mixture.		Number of Individuals Used.	Time Left in Mixture.	Condition after the Experiment.
Sea Water.	Fresh Water.			
1	1	1	3 hours.	Good.
1	2	2	1 hour.	Both good.
1	2	2	4 hours.	Both good.
1	2	2	24 hours.	Both good.
1	3	2	1 hour.	Both lived, but were in poor condition.
1	4	3	Until dead.	Died in 5–6 hours.
0	1	2	3 hours.	Recovered somewhat, but died within 3 days.

As will be seen from the table, animals which were left for twenty-four hours in a solution which consisted of one third sea water and two thirds fresh water, were apparently uninjured; while individuals which were immersed in fresh water for three hours died. Mr. E. D. Congdon's observations on this species are of interest in this connection. He told the writer that he had found *Thyone briareus* at the mouths of rivers in water which was half salt and half fresh, as judged by the specific gravity, but it was never found any farther up rivers than that.

5. *Light Stimulation.* — *Thyone* is extremely sensitive to a decrease in the light intensity and what may be called the "shadow" reaction is one of its most characteristic responses. If an individual is resting quietly in the sand with only the posterior end of the body exposed and the experimenter's hand is passed between it and the window, it at once withdraws the visible portion of the body. This response is of course variable and it may not occur at all or it may be so pronounced that the animal completely disappears beneath the sand. The same withdrawal is induced if a shadow is thrown on the anterior end or even on one tentacle and a particularly sensitive individual was caused to contract by extending a pencil over the top of the beaker in which it lay.

Although such characteristic responses are given when the light intensity is decreased no reaction occurs when there is a corresponding increase. An individual will contract at once when an object is interposed between it and the light, but it gives no response if the object is removed after a time. Furthermore, when light from a large oil lamp or from the sun was suddenly reflected from a mirror on a feeding individual there was no response. This sensitiveness to decrease in the light intensity and lack of response to an increase is similar to the reactions observed by Hargitt (:06) in *Hydroides dianthus* and other annelids. Uexkull ('97) has also described striking shadow responses in sea-urchins.

Thyone gives well-marked locomotor responses to light which may be illustrated by the following experiment: Eight individuals were successively placed in a shallow rectangular glass dish which measured 29 cm. long by 25 cm. wide, and contained sea water. The dish was enclosed in a black box which had an opening at one end. This opening was directed toward the window so that light was admitted from only one direction. The animals were always placed with the long axis of the body at right angles to the light rays and the direction of the subsequent movement was then observed. In a series of twenty-four reactions the locomotion in every case carried the animal away from the light to the end of the dish, but there was no definite orientation of the body in relation to the light. In ten of these negative responses the anterior end was ahead as the individual moved; in nine instances the posterior end preceded the anterior; and in five the locomotion was straight toward the right or left. Not one of the eight individuals moved in every case with the anterior or posterior end in front.

The influence of the negative light response is also apparent in the righting reactions. When individuals were placed in the same position as in the experiments described in the last paragraph, except that the ventral side of the body was uppermost, the righting reaction usually carried the ventral surface away from the light. Two individuals were given fifteen trials each in the manner just described, the anterior end being turned alternately toward the right and left in successive trials. One of them turned four times toward the light in righting itself and

the other turned only three times in that direction. In other words, twenty three out of thirty reactions (77 per cent.) were away from the light.

Another reaction which shows a negatively phototropic response is apparent when an animal burrows next the side of a glass vessel. It never remains against the glass but moves out into the sand after it has covered itself. This action is without doubt due to light stimulation for an animal will remain indefinitely in contact with an opaque object, such as a stone.

These reactions show that the *Thyone* is sensitive to decreased light intensity, and that it is negatively phototropic but without any definite orientation of the body to the source of the illumination, or the direction of the rays. This lack of orientation is rather striking in a bilaterally symmetrical animal and it shows that the response is not brought about in this case by unequal stimulation on the right and left sides of the body.

6. *Heat Stimulation.* — *Thyone* was not found to be very responsive to temperature changes, and individuals lived for several days at room temperature (24–28° C.) without apparent injury. Attempts were made to induce reactions by local changes in the temperature. The method was to siphon boiling water or a mixture of ice and salt water through a small U-shaped glass tube which could be brought close to the surface of the individual to be tested. Although six different animals were each tried twice with the hot tube and twice with the cold tube by holding the tube less than a millimeter below the extended posterior end, not a single response was observed.

Attention was next turned to the effects of an increase or decrease in temperature which affected the whole body. To test the effect of increased temperature six individuals (which were buried in the sand at the bottom of separate beakers containing sea water) were placed two at a time on a sand-bath and slowly heated. All the animals became active after the temperature had reached 30° C. The tube-feet were waved about on all sides and the body began to execute irregular twisting movements which continued until the temperature was lowered again. Two of the individuals were slowly heated to 36.5° C., the time required to reach that temperature being one hour and thirteen

minutes. One of these animals soon died but the other was in excellent condition four days afterward. Two other animals were heated to 41° C. during two hours and thirty-eight minutes and both of them died, although one continued to contract slowly when poked for two days. The two remaining individuals were heated to a temperature of 37° C. during two hours and forty minutes. Next day they were both in excellent condition and gave good burrowing and shadow reactions.

In order to test the effect of decreased temperature, beakers containing buried individuals were placed in a pail of cracked ice and salt and allowed to remain until the temperature had been sufficiently lowered. A beaker containing one animal was placed in the "freezer" and when the temperature had reached + 8° C. it failed to give the shadow response but contracted somewhat when the beaker containing it was jarred. In two hours and twenty minutes the sand was frozen solid and covered over with ice crystals. A thermometer held against the body of the animal registered — .5° C. At this temperature the posterior end still contracted when poked. Twenty minutes later with the temperature at — 1.6° C. only a feeble contraction was induced by poking, and after thirty minutes more the whole body was stiff and apparently frozen solid. The animal was left an hour longer and became completely covered over with ice crystals. The beaker was then removed, after having been in the freezer four hours and twenty minutes. The animal was found to be dead after the ice thawed. Another beaker which contained two *Thyones* was introduced into the freezer. Both these individuals were buried in the sand and covered by sea water. The temperature was reduced so that the sand was frozen and a thermometer resting against one of the animals registered — 2° C. to — 3° C. for two hours and forty minutes. After having been in the freezer three hours and forty minutes the beaker was removed. Twelve hours later both the individuals it contained had cast out the viscera but they did not die and continued active for several days, though they were in poor condition and gave no shadow reaction. Grave (:05) observed that *Cucumaria* retracted the whole body during cold weather and Mr. George Gray had informed me that *Thyone* buries itself six or eight inches in the sand

during the winter. I had therefore expected to see the burrowing reaction take place as the temperature was reduced but all three of the individuals remained perfectly quiet as the ice formed around them and the posterior end was not withdrawn.

From the experiments described it is evident that *Thyone* is comparatively insensitive to thermic changes and that it is able to react through a wide range of temperatures. The maximum and minimum vital limits are in the neighborhood of 40° C. and 0° C. respectively.

VIII. Experiments to Determine whether the Integrity of the Nervous System is Essential to Reactions.

The classical work of Romanes ('85) showed that a single fifth of the body wall of a sea-urchin was able to carry on locomotion without any of the visceral organs. Such fragments executed righting reactions and showed the same positive phototropism which was characteristic of entire animals. Mead (:01) kept detached starfish arms alive for as much as three months and they retained their powers of locomotion and gave the usual righting reaction. Von Uexkull ('97) found that pieces of sea-urchin would react to mechanical stimulation but the responses to shadows depended on keeping the system of radial nerves intact. These and other observations show that the nervous system of the asteroids and echinoids is little centralized in some respects, though Jennings (:07) has recently described some remarkable instances of association in the starfish. Clark ('99) found that cutting the oral nerve ring made no appreciable difference in the reactions of *Synapta*. Henri (:03, :03*a*, :03*b*) showed that nerve centers exist in the radial nerve trunks of *Stichopus regalis* and that reflex muscle contractions could be induced through them by stimulating the skin. He states that such radial nerve centers control only a limited portion of the body musculature and that reflexes which involve more than one of the longitudinal muscles must pass through the oral nerve ring.

As has been stated, the nervous system of holothurians consists of a circum-oral ring which gives rise to five radial nerve trunks and these are connected through their finer branches which anastomose to some extent. This system has been modified some-

what to conform to the bilateral plan of structure and, as the radial nerves are not equally well developed, there is a dorso-ventral as well as an antero-posterior differentiation. In order to test the reactions of fragments of the body a series of experiments was carried out in which twelve *Thyones* were each divided into two approximately equal pieces by a transverse cut. The two pieces of each animal were laid in a dish of sea water before a window in the position shown in Fig. 6. The ventral side of

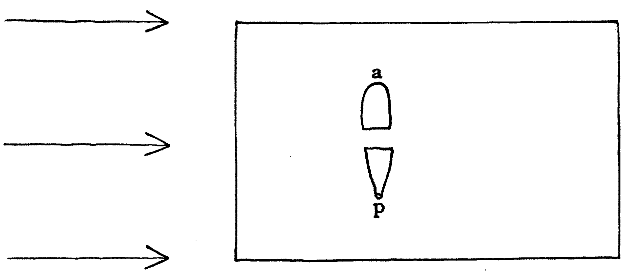

FIG. 6. Diagram to show the position in which animals were placed in the dish after being cut in two. The arrows represent the direction of the light. *a*, anterior end ; *p*, posterior end.

the body was always placed uppermost and the long axis of the body was at right angles to the direction of the rays of light. The movements of the two halves were observed during the three hours following their separation and a summary of these reactions is given in Table III. Although the tube-feet were more or less

TABLE III.

Showing the number of anterior and posterior halves of twelve *Thyones* which gave different reactions.

Nature of Reaction.	Locomotion.				Righting.	Shadow.
	Toward Light.	Away from Light.	Straight Ahead.	None.		
Number of anterior halves reacting....................	3	2	2	5	11	3
Number of posterior halves reacting....................	4	7	0	1	12	9

active on both halves of the body in all cases, it will be seen that the posterior halves gave characteristic reactions more often than the anterior portions. They carried on normal spouting move-

ments and performed the righting reaction more rapidly than the anterior halves. The only response in which the anterior half approached the posterior in the number of individuals which responded was in the righting reaction. This was probably due, in part at least, to the structure of the tube-feet which have more efficient sucking discs on the ventral than on the dorsal surface, and those on the ventral side would hence be more likely to become attached if all of them were active. Two of the individuals were kept in a dish without changing the water for three days after they had been bisected. Both the posterior halves remained in good condition and gave characteristic shadow responses at the end of the third day, but both the anterior portions threw out the viscera during the second day and were dead on the third day.

These experiments show that the presence of the circum-oral nerve ring is not essential for the performance of correlated reactions and that the posterior half of the body is apparently able to carry on movements better than the anterior. This greater efficiency shown by the posterior end of the body is perhaps what might be expected from the fact that the whole anterior portion is often cast off and dies while the posterior end lives and regenerates the lost organs. These conclusions do not agree with those reached by Henri (:03*b*) from his work with *Stichopus regalis*. He believed that the oral nerve ring was necessary for general muscular reflexes.

IX. Variability of Reactions.

Few of the reactions which have been described in this paper could always be induced by a repetition of a stimulus which had previously brought them about. The response which was perhaps the most unfailing was the contraction of the body which resulted from gentle mechanical stimulation with some pointed object, but even this response varied with the strength of the stimulus, the condition of the individual and other factors. Not only did characteristic responses often fail to take place after a stimulus but they were sometimes modified so that they did not take place in the usual manner. Such differences in reactions may be due to internal causes which have to do with the structure or the past experience of the individual, or they may be caused by various

external factors. It is important to discover, if possible, what stimuli will cause these differences in behavior. When *Thyone* extends its tentacles and feeds, the movements are brought about by such factors as hunger, or the presence of food, or by a combination of two or more such stimuli. If we throw a shadow on it as it feeds, the tentacles contract and the withdrawing reaction takes place. Although all the stimuli which were effective in producing the feeding reaction but a moment ago are present and acting, we have introduced an additional stimulus which has modified the response. This is an example of inhibition, as the presence of one stimulus inhibits the response to certain other stimuli. The periodic repetition of a stimulus is another means by which responses may be changed. As Jennings (:05) says of this method "the physiological state tends to resolve itself into another and different state" after a stimulus has been received. An individual will be in a different condition, and will really be a different animal, after it has received the first stimulus and may therefore give a different response the second time the same stimulus is received. Some of the instances of variable behavior which were observed will now be briefly considered.

1. *Repetition of a Stimulus.*— Responses usually vary in degree when a stimulus is repeated at regular intervals. If an individual is touched gently with a glass rod and then touched again on the same spot at one minute intervals the withdrawing response which was at first marked becomes gradually weaker and finally ceases altogether. Similar results may be obtained by allowing a drop of water to fall at regular intervals into the dish which holds an animal, or by periodically throwing a shadow upon an extended individual. By increasing the interval of time between successive stimuli a larger number of responses may be obtained but the result will be the same in the end. Individuals which have been newly brought from the ocean contract at the slightest disturbance and give the withdrawing reaction whenever anyone walks across the floor or opens a door or when any other slight change occurs in their surroundings, but they soon cease to respond to such stimuli. For example, one individual which had been kept for two weeks on a table in the laboratory carried on normal feeding and breathing reactions while people were con-

stantly passing between it and the window. After this animal had been allowed to remain in a quiet situation in another room for a week however it had again become extremely sensitive to shadows, jars, currents of water and other gentle forms of stimulation.

Thyone sometimes modified its behavior after a stimulus had been repeated several times and a new form of response occurred. On one instance an individual which had been used in previous experiments was stimulated by gently sticking a glass rod among the tentacles as it was feeding. At first all the tentacles were withdrawn as soon as the rod touched one of them, but after the fourth trial they were no longer retracted, and when the rod was pressed gently against the mouth the anterior end was turned to one side but not withdrawn. This change in response was brought about in half an hour.

2. *Inhibition.* — As has been stated, the shadow reaction was one of *Thyone's* most constant and characteristic types of response but it would not take place if certain stimuli were present. To give some specific instances : This reaction was inhibited when the temperature of the water fell below 10° C., when the posterior end was greatly elongated toward the surface on account of stagnant water, and after the respiratory movements had been prevented from occurring for some time. In all these cases individuals gave characteristic shadow responses before and after the inhibiting stimulus was present. Another characteristic reaction was locomotion away from the light, but, when an animal was against the side of a glass vessel it often moved at right angles to the direction of the light rays, the thigmotactic stimulus being more potent than the light. Furthermore, if an individual was laid on its dorsal surface with the median plane inclined slightly toward the source of the illumination, it often moved one or two centimeters toward the light in righting itself. These instances are typical of others which might be given and they show that though *Thyone's* responses are largely of a stereotyped nature, they are interrelated in such a way that one may inhibit another.

X. General Considerations.

Thyone briareus is a holothurian which is rather strikingly adapted to a sedentary life. It is not able to change its place of abode easily and it is hence highly resistant to unfavorable conditions in its environment. Individuals which were allowed to lie on moist sand exposed to the air for eighteen hours were apparently uninjured. This tenacity to life is also shown by the ability this species manifests to withstand changes in the temperature and the density of the water in which it lives. The methods of feeding, locomotion, respiration and other activities are adapted to the peculiar conditions under which it exists. Passing most of its life buried in the mud, *Thyone* probably does not often fall a prey to large enemies but it is protected from them by the withdrawing reaction, by its locomotion away from the light and by its habit of pulling pieces of eel grass and other debris over the body.

Many of *Thyone's* movements show a lack of correlation. In ordinary locomotion on a solid surface, the tube-feet which are behind are often forcibly pulled loose from their attachments instead of being released by means of some impulse from the central nervous system. Such organs as the tube-feet are able to work more or less independently, but they may also be actuated by a unified impulse, as is shown when they are simultaneously extended or contracted over the whole body and the same unity is apparent in their action as they pull the animal along in a definite direction. On the other hand many reactions show considerable power of correlation and adaptation. Correlation is shown in the use of the circum-oral tentacles, as they move in a rather definite order. Very often, however, two of them endeavor to enter the mouth at the same time, but one always bends aside to make way for the other. If the correlation in the movements was perfect in this case, two tentacles would not try to enter the mouth at once, and if there was no correlation they would struggle with each other indefinitely. Furthermore, when a feeding individual lies on its side, the tentacles which scrape the bottom are used oftener than the others and there is thus an increased chance of obtaining food.

Generally speaking, it may be said that *Thyone's* hehavior,

like that of other sedentary animals, is mostly made up of stereotyped reactions which occur regularly in response to certain stimuli. Furthermore, many of these reactions are carried on independently by certain separate organs and two parts of the body may "work against each other" for a time, but, under the proper conditions of stimulation, all these simpler reactions may be unified into one general correlated response. Although the reactions are largely stereotyped in nature they may be changed by experience or inhibited by the presence of different stimuli. The stereotyped methods of response are usually adequate to meet the conditions under which *Thyone* exists and would usually enable it to survive in the struggle for existence. If they are not adequate, however, they may be modified to meet new conditions. For example, this species usually burrows into the mud so that only the posterior tip of the body is exposed and even this is withdrawn if the slightest shadow falls upon it or if the water is agitated. If the water becomes stagnant the same individuals that were formerly so reactive will climb up the side of the jar and cease to respond to such slight stimuli as shadows and water currents, and they contract only when touched by some solid object. As the water becomes foul, the greatest need of the organism is oxygen and the behavior described would enable this to be obtained, but to accomplish this end, the animal would be obliged to forego the temporarily less important matter of protection from its enemies.

When compared with an echinoid or a star-fish as described by Romanes ('85) and Jennings (:07), or with an ophurian as it is represented by Glaser (:07) *Thyone* falls short in the range and diversity of its reactions. This is probably due in part to its sedentary mode of existence and the study of holothurians which do not burrow might show a somewhat different set of reactions. Perhaps the most interesting point which is brought out in the study of *Thyone's* behavior is the fact that, although the symmetry is so strikingly bilateral, the locomotion is carried on with the same lack of orientation which is so characteristic of other groups of echinoderms.

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